



Four new records of gymnosome pteropods (Pteropoda, Gymnosomata) in the Campeche Canyon, southern Gulf of Mexico

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Abstract. This study reports four new records of gymnosome pteropods (Pteropoda, Gymnosomata): *Pneumodermopsis macrochira* Meisenheimer, 1905, *Spongiobranchaea intermedia* Pruvot-Fol, 1926, *Schizobrachium cf. polycotylum* Meisenheimer, 1903, and *Cliopsis krohnii* Troschel, 1854, collected at different depths in the Campeche Canyon, southern Gulf of Mexico, during the winter storm season in 2011 (“Nortes”). These species are illustrated and described, increasing the knowledge of this group in the region. We also present hydrographic conditions of the stations and depths where the organisms were collected.

Key words. Zooplankton, gymnosomes, species richness, diversity, “Nortes” season

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INTRODUCTION

The marine zooplankton includes a highly diverse group of small organisms distributed around the world's oceans. They play a key role in the carbon and energy transfer through the pelagic food web, contributing to the functioning of the biological pump (Brierley 2017). As one of the members of the marine zooplankton, pteropods are a group of organisms highly abundant and keystone species in any marine ecosystem due to the multiple ecological roles they play. For example, due to their different feeding habits (omnivores, herbivores, and carnivores) they prey on a wide variety of organisms, which promotes the carbon and energy transfer throughout the pelagic trophic web (Peijnenburg et al. 2020). Besides that, due to their small size (0.5–5.0 mm length), they are attractive prey for a variety of animals, such as fishes, sea turtles, jellyfishes, and even whales, but gymnosome pteropods can also be predators of other organisms, such as copepods or salps (Lalli and Gilmer 1989). Pteropods are characterized by having a foot modified into two paired swimming wings. Pteropoda is composed by three suborders, Euthecosomata, Pseudothecosomata, and Gymnosomata (Bouchet et al. 2017); the last one includes species with a cylindrical or globose body and without a shell in their adult stage (van der Spoel 1996; van der Spoel and Dadon 1999), and it is divided into the superfamilies Clionoidea and Hydromyoidea (Bouchet et al. 2017). Gymnosomes are active predators with specialized feeding structures such in the buccal mass such as hooks, sticky glands, and sucker arms (van der Spoel, 1996), and they may be hermaphrodites at maturity (Lalli and Gilmer 1989). Recent studies suggest that pteropods (including gymnosomes) are under a serious threat due to the anthropogenic activities that affect the health of marine ecosystems. It has been documented that the alterations of pH levels (that generate acidification scenarios) negatively affect the calcification of pteropods in sub-Antarctic (Mekkes et al. 2021a) and subtropical waters (Mekkes et al. 2021b), producing smaller organisms with thinner shells. So, pteropods are now considered as proxies of ocean acidification conditions, and they have even been regarded as “the canary in the coal mine” (Oakes et al. 2021). Under this scenario, investigations on pteropods could be helpful in studies aimed to establish a baseline condition essential for any marine ecosystem.

In Mexican waters of the southern Gulf of Mexico, pteropods occur in high abundance (Toral-Almazán et al. 2022). Since the 1970s the importance of these organisms has been highlighted thanks to the efforts



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carried by the Mexican government in one of the first oceanographic monitoring programs in the region (Toral-Almazán et al. 2022). The southern Gulf of Mexico also hosts a high species richness that has seasonal fluctuations. Suárez and Gasca (1992) recorded 15 species during the coldest month of the year (January), when *Creseis acicula* (Rang, 1828) was the dominant species followed by *Heliconoides inflatus* (d'Orbigny, 1835), *Limacina trochiformis* (d'Orbigny, 1835), and *Diacavolinia longirostris* (Blainville, 1821).

Studies carried out in the last decade confirmed the high species richness of the southern Gulf of Mexico. Flores-Coto et al. (2013) analyzed the pteropod community structure during August, identifying 18 species, with *C. acicula* as the dominant species. Lemus-Santana et al. (2014) recorded 27 pteropod species during May and November, with dominance of *Creseis virgula* (Rang, 1828), *C. clava* (Rang, 1828) [currently referred to as *C. acicula* (Rang, 1828)], *L. inflata* (d'Orbigny, 1834) [currently referred to as *Heliconoides inflatus* (d'Orbigny, 1835)], and *L. trochiformis* (d'Orbigny, 1835). López-Arellanes et al. (2018) found 29 species during two spring seasons and stated that *Creseis conica* Eschscholtz, 1829 was the dominant species. More recently, López-Cabello et al. (2022) reported 18 species in pelagic waters of the Campeche Canyon in the southern Gulf of Mexico during February, with the highest density value for *L. trochiformis* (d'Orbigny, 1835). Studies including species belonging to the suborder Gymnosomata in the Gulf of Mexico documented *Pneumoderma violaceum* d'Orbigny, 1835 in May (Lemus-Santana et al. 2014), and *Cephalobrachia macrochaeta* Bonnevie, 1913 in May and August (Flores-Coto et al. 2013; Lemus-Santana et al. 2014), while *Clione limacina* (Phipps, 1774), *Paracptune longicaudata* (Souleyet, 1852), and *Thliptodon diaphanus* (Meisenheimer, 1902) were documented in May and June by López-Arellanes et al. (2018). Additionally, *P. violaceum* d'Orbigny, 1835 and *P. longicaudata* (Souleyet, 1852) were recently reported in February (López-Cabello et al. 2022).

All the investigations carried out so far in the southern Gulf of Mexico have been very important in documenting the species richness of the region. However, a complete characterization of the pteropod community structure in the southern Gulf of Mexico is far from achieved. Most of the studies are restricted to the warm season (May to September) and mostly to species of the suborder Euthecosomata, so there are still some gaps in knowledge about species richness during the coldest months of the year (January–February) and particularly of pteropods belonging to the suborder Gymnosomata. Besides that, in most cases, no illustrations or descriptions have been provided, hampering comparisons among populations.

In this study we report for the first time in the Campeche Canyon, southern Gulf of Mexico, four species of pteropods belonging to the suborder Gymnosomata collected in February 2011. The species described and documented here represent new records for the region. This study complements previous research, fills gaps of diversity and distribution of gymnosomes, particularly for the coldest season of the year, and provides an overview of the specific depths in which these organisms are vertically distributed.

METHODS

Study area. The Gulf of Mexico is a large, deep interior sea located in the eastern North American continent. Its waters are shared by three countries, the United States of America, Cuba, and Mexico (Figure 1B). The gulf is a highly dynamic ecosystem, with different oceanic processes, from the microscale (e.g. internal waves), the mesoscale (e.g. eddies) to the macroscale (e.g. the Loop current system), which are linked to the supply of nutrients towards the euphotic layer that stimulates biological production (Durán-Campos et al. 2017). Three climatic seasons are recognized in the gulf. The dry season is from March to May, the wet season from June to October and the “Nortes” season from November to February (Contreras-Ruiz et al. 2014). The latter is characterized by the presence of strong and persistent northerly winds (>80 km/h), with the most intense events usually between January and February, that induce changes in the hydrographic properties of the water column, including a deeper mixing layer (>70 m depth) (Arriola-Pizano et al. 2022).

Fieldwork. The biological material used in this study was collected during the oceanographic research cruise “CAÑON-IV” developed in the waters of the Campeche Canyon, southern Gulf of Mexico, in February 2011 (“Nortes” season), onboard the R/V Justo Sierra operated by the National Autonomous University of Mexico.

Four stations (Figure 1C) were sampled (both day and night; see Table 1) at different depths using conical nets (505 µm mesh, 0.75 m diameter of mouth) configured with mechanical flowmeters (General Oceanics Inc. 2030R) in a close/open/close system. The closed nets were deployed at 10, 50, 100, and 200 m depth calculating the cosine of the wire angle (Kramer et al. 1972). Each net was opened using manual messengers (Go-devil, 31 oz Bronze) to haul for 15 min at a speed of 2 knots. Once the time finished, the nets were closed again with manual messengers and retrieved to the deck where they were carefully inspected and rinsed with seawater to recover the collected organisms. Immediately, the organisms were fixed with a 4% formaldehyde solution with added borax for 24 h. After it, the samples were transferred to a 70% ethanol solution in glass jars with hermetic lids for their final preservation. One of the main advantages of using this solution as a fixative agent is that it allows zooplankton samples to be preserved for several years without damaging the body or body tissue of organisms (Santhanam et al. 2019). During the storage time, the ethanol in the jars was replaced continuously, every two months, to avoid evaporation of the solvent and damage to the specimens.

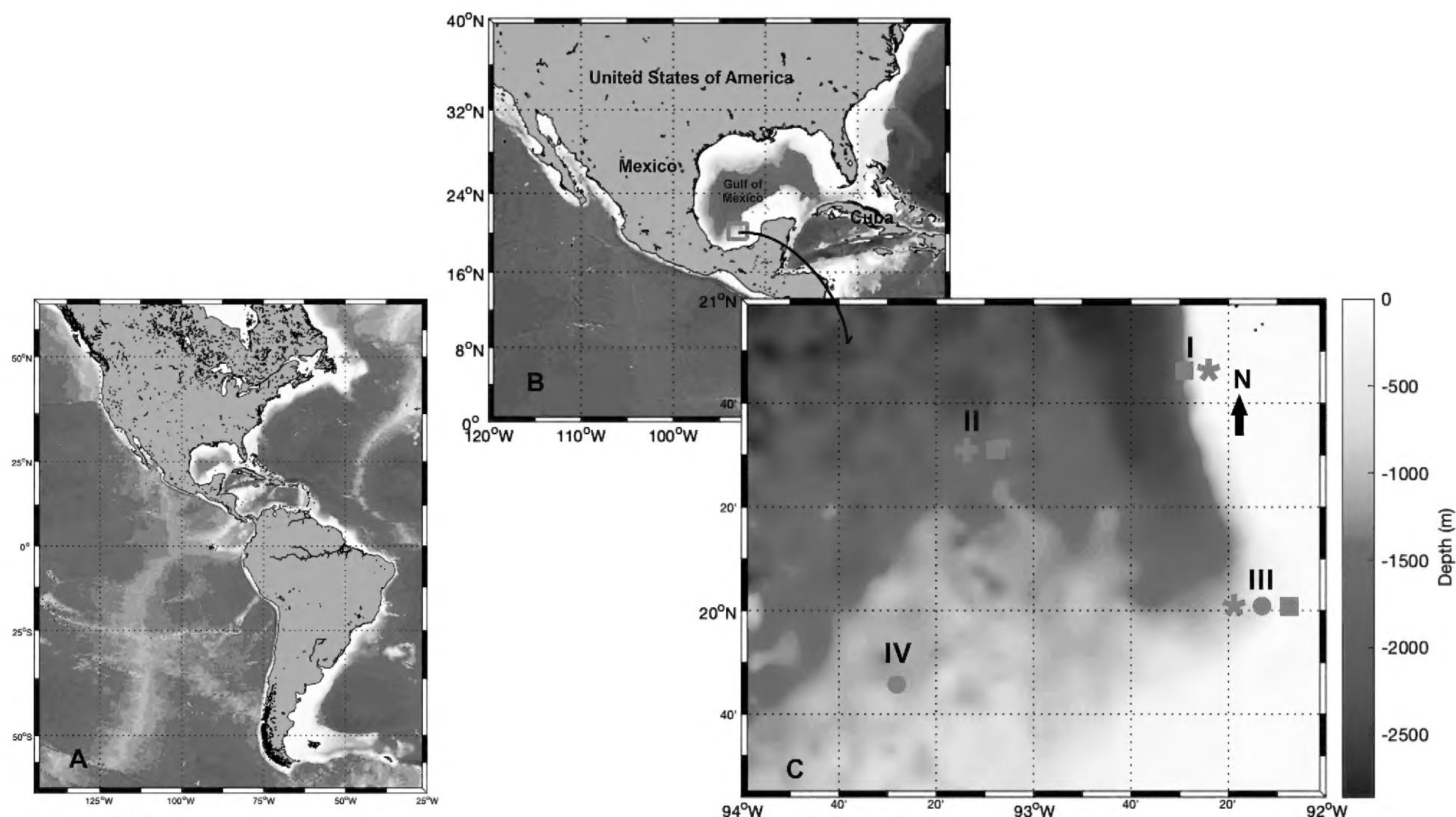


Figure 1. **A.** Map showing localities (★ red symbols) where *Pneumodermopsis macrochira*, *Spongiobranchea intermedia*, *Schizobrachium polycotylum*, and *Cliopsis krohnii* have been previously reported in the American continent (e.g. Dadon and Chauvin 1998; Larrazábal and Solares-de-Oliveira 2003; Seibel et al. 2007; Bucklin et al. 2010; Jennings et al. 2010; Angulo-Campillo et al. 2011; Moreno-Alcántara et al. 2014; Angulo-Campillo and Aceves-Medina 2018). **B.** Study area in the Gulf of Mexico. The rectangle in red shows the Campeche Canyon. **C.** Sampling area; symbols indicate localities where the four newly recorded of pteropods were collected: *Pneumodermopsis macrochira* (★), *Schizobrachium cf. polycotylum* (★), *Spongiobranchea intermedia* (●), and *Cliopsis krohnii* (■).

To have an overview of the physical configuration of the water column where the organisms were collected, high-resolution hydrographic data were acquired with a Conductivity-Temperature-Depth probe (CTD, SeaBird 19 plus) equipped with a chlorophyll-*a* fluorescence and a dissolved oxygen sensor (ECO-Wet Labs and SeaBird 43, respectively). Each CTD cast was near the bottom (10 m) with the equipment configured to acquire data at 24 Hz.

In the laboratory, pteropods were separated in a glass petri dish and identified at species level using a Zeiss Stemi 508 stereomicroscope configured with an Axiocam ERc and identification keys (e.g. Tesch 1950; van der Spoel and Dadon 1999). The species identification was confirmed through international repositories (e.g. MolluscaBase, Tree of Life Project). Photographs of each specimen were taken in different views and processed with Helicon Focus v. 8.2.0 (Helicon Soft Ltd.) and Adobe Photoshop v. 23.5.1 (Adobe Inc.) software. It is important to note that the well preservation of the organisms allowed us to observe diagnostic taxonomic structures for the determination of the species, such as oral structures, pedal lobes, anterior and posterior gills, as well as the evident differentiation between the proportion and arrangement of the body. Due to the above and the small number of organisms available for each species (see details in Table 1), the dissection of internal structures (e.g. extraction of the arms, suckers, and radula) was not considered in this study; rather, we prefer to keep undamaged organisms in a scientific collection for future reference. In this sense, and particularly for one taxon (*Schizobrachium polycotylum* Meisenheimer, 1903) we present a provisional identification. The last is related to the need for further detailed dissections and by the presence of chromatophores and, possibly, other features that were not completely described.

In terms of the physical data acquired with the CTD casts, they were processed following the manufacturer's standard protocols, finally averaging each meter. The temperature (°C), salinity (g/kg), and density of seawater (σ_t, kg/m³) were derived with the thermodynamic equation of seawater 2010 equation (IOC et al. 2010).

RESULTS

The hydrographic conditions of the water column at each station at each sampling depth were quite different (Table 1). At the surface (10 m depth), temperature ranged from 23.83 to 24.50 °C, salinity from 35.99 to 36.37 g/kg, σ_t from 24.10 to 24.58 kg/m³, chlorophyll-*a* ranged from 0.12 to 0.17 mg/m³, while the dissolved oxygen ranged from 4.42 to 4.34 mg/L. The temperature values decreased as the depth increased, while the density values increased. At 50 m depth, the temperature values ranged from 22.85 to 22.99 °C, the

Table 1. Individuals of *Pneumodermopsis macrochira* Meisenheimer, 1905, *Spongiobranchaea intermedia* Pruvot-Fol, 1926, *Schizobrachium* cf. *polycotylum* Meisenheimer, 1903 and *Cliopsis krohnii* Troschel, 1854 in the Campeche Canyon, southern Gulf of Mexico, during the winter storm season in 2011 (“Nortes”) at each station and sampling depth, with some hydrographic conditions. Abbreviations are: Chl-a = chlorophyll-a, DO = dissolved oxygen, ND = not detectable.

	Station I (50 m depth)	Station I (100 m depth)	Station II (200 m depth)	Station III (10 m depth)	Station III (50 m depth)	Station IV (10 m depth)
Sampling hour	9:20	09:20	04:25	04:10	04:10	18:12
Temperature (°C)	22.85	18.58	14.31	23.83	22.99	24.35
Salinity (g/kg)	36.83	36.58	36.02	36.37	36.83	35.99
σt (kg/m ³)	25.21	26.19	26.77	24.58	25.17	24.10
Chl-a (mg/m ³)	0.93	0.04	ND	0.12	0.41	0.17
DO (mg/L)	4.53	4.36	3.89	4.42	4.43	4.34
<i>Pneumodermopsis macrochira</i>	—	—	1	—	—	—
<i>Schizobrachium</i> cf. <i>polycotylum</i>	1	1	—	1	—	—
<i>Spongiobranchaea intermedia</i>	—	—	—	—	4	3
<i>Cliopsis krohnii</i>	1	1	1	1	2	—

σt values ranged from 25.17 to 25.21 kg/m³ while the salinity was 36.83 g/kg. At this depth, chlorophyll-a values increased in a range from 0.41 to 0.93 mg/m³, while the dissolved oxygen values ranged from 4.43 to 4.53 mg/L. At 100 m depth, the temperature value was 18.58 °C, the salinity of 36.58 g/kg, σt was of 26.19 kg/m³ while the chlorophyll-a was barely 0.04 mg/m³ and dissolved oxygen was of 4.36 mg/L. At 200 m depth, the temperature was lower, with 14.31 °C, the salinity value was of 36.02 g/kg, σt was of 26.77 kg/m³, the chlorophyll-a was not detectable, and the dissolved oxygen was 3.89 mg/L.

In addition to previously records of pteropod species in the Campeche Canyon (López-Cabello et al. 2022), four species of pteropods belonging to Gymnosomata were recorded for the first time: *Pneumodermopsis macrochira* Meisenheimer, 1905 (Figure 2), *Spongiobranchaea intermedia* Pruvot-Fol, 1926 (Figure 3), *Schizobrachium* cf. *polycotylum* Meisenheimer, 1903 (Figure 4), and *Cliopsis krohnii* Troschel, 1854 (Figure 5).

Spongiobranchaea intermedia was the most abundant species (with seven individuals), recorded in two stations at two depths: station III at 50 m and station IV at 10 m. The second most abundant species was *C. krohnii* (six individuals) at four different depths (10, 50, 100, and 200 m) in three stations (I, II, and III). *Schizobrachium* cf. *polycotylum* was found at two stations at different depths, the station I at 50 m and 100 m depth, and the station III at 10 m depth, amounting three individuals. The least abundant species was *P. macrochira* (only 1 individual), founded at station II at 200 m depth (Table 1).

Order Pteropoda
Suborder Gymnosomata
Superfamily Clionoidea
Family Pneumodermatidae

***Pneumodermopsis macrochira* Meisenheimer, 1905**

Figure 2

Material examined. MEXICO – SOUTHERN GULF OF MEXICO • Campeche Canyon; 20.5°N, 093.25°W; 200 m depth; 25.II.2011; E. Coria-Monter and E. Durán-Campos leg.; CC2011-1n.

Identification. Organism with 2 mm long, mainly colorless, with the visceral mass evident through the body wall, filling it completely. Two lateral arms, with up to 55 suckers on each arm, the top arm is larger than the other, similar in structure. A posterior gill is evident. Median footlobe relatively long, which gives mobility to swim and hunt efficiently. The most typical features for this species are the sucker arm and posterior gill. The posterior gill includes four crests radiating from the body pole. This organism is in a young stage, the crest of posterior gill beginning to be visible. The median footlobe is pointed and long, and a median tubercle is present. The median sucker arm is reduced and represented by five relatively long-stalked suckers. The hook sacs are shallow. Although the body is colorless, purple-gray chromatophores can occasionally be seen.

Distribution. Oceanic, epipelagic in tropical, subtropical, temperate, and sub-Antarctic environments. Atlantic and Indian Oceans. North Pacific and Tasman Sea (Larrazábal and Solares de Oliveira, 2003; Bucklin et al. 2010; Jennings et al. 2010; Angulo-Campillo et al. 2011; Angulo-Campillo and Aceves-Medina 2018).

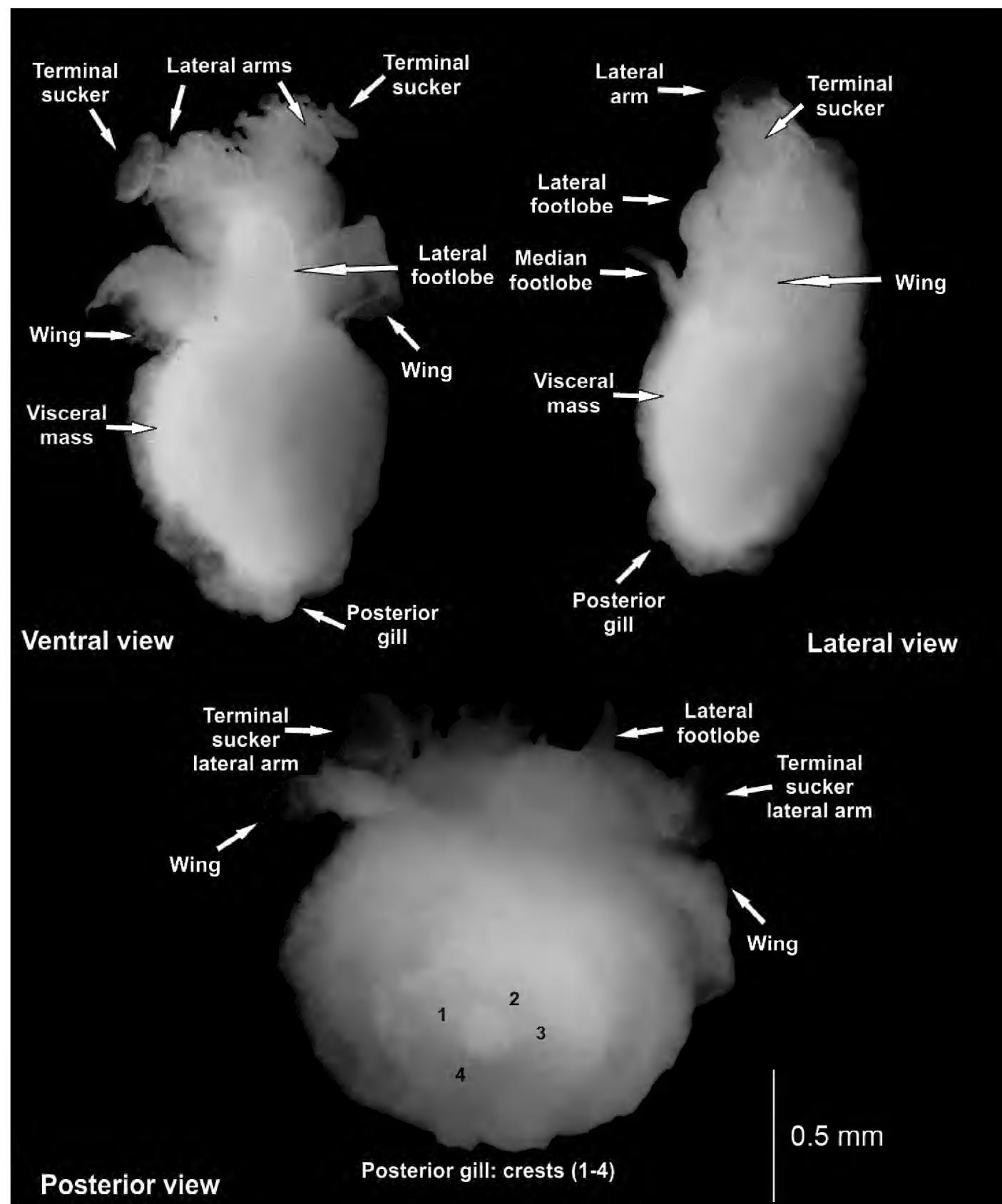
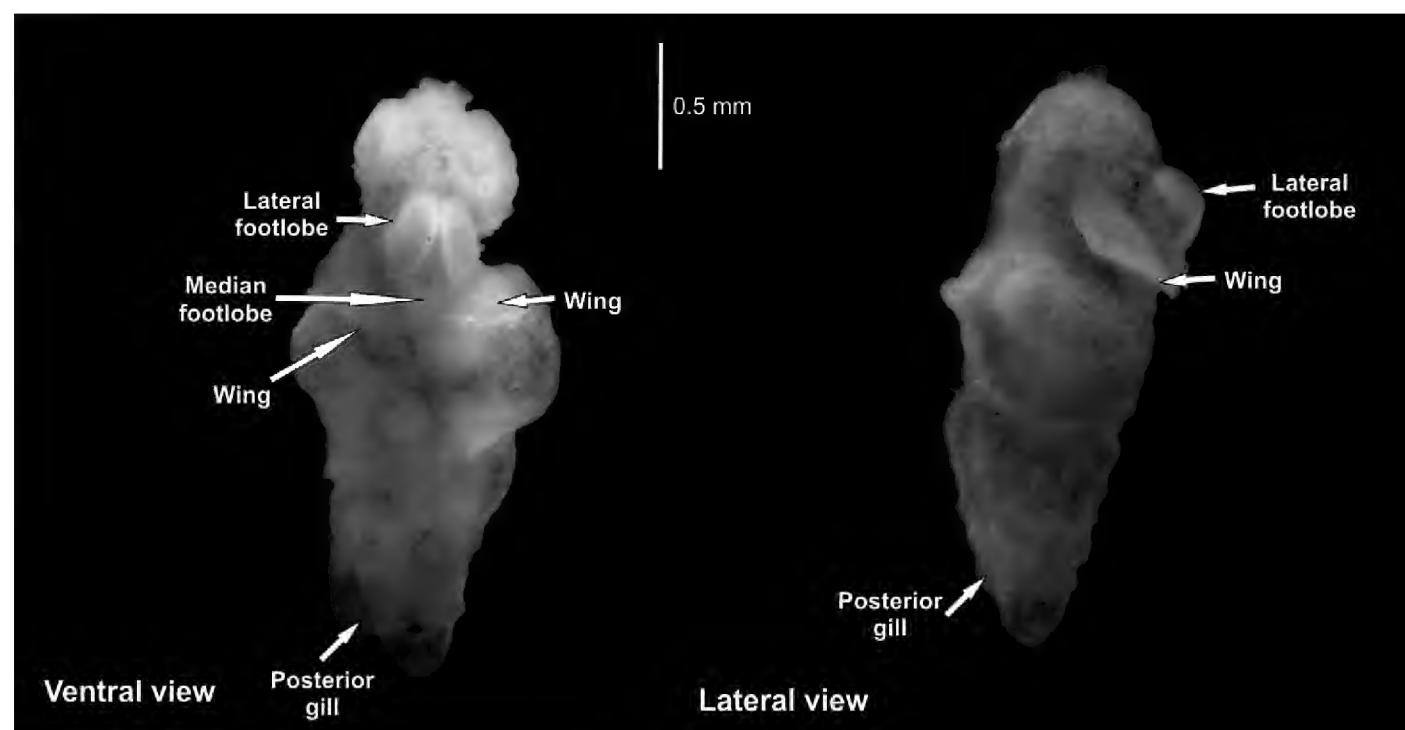


Figure 2. *Pneumodermopsis macrochira* Meisenheimer, 1905 (3 views). White arrows indicate diagnostic characteristics that allowed for identification of this species.

Figure 3. *Spongiobranchaea intermedia* Pruvot-Fol, 1926 (2 views). White arrows indicate diagnostic characteristics that allowed for the identification of this species.



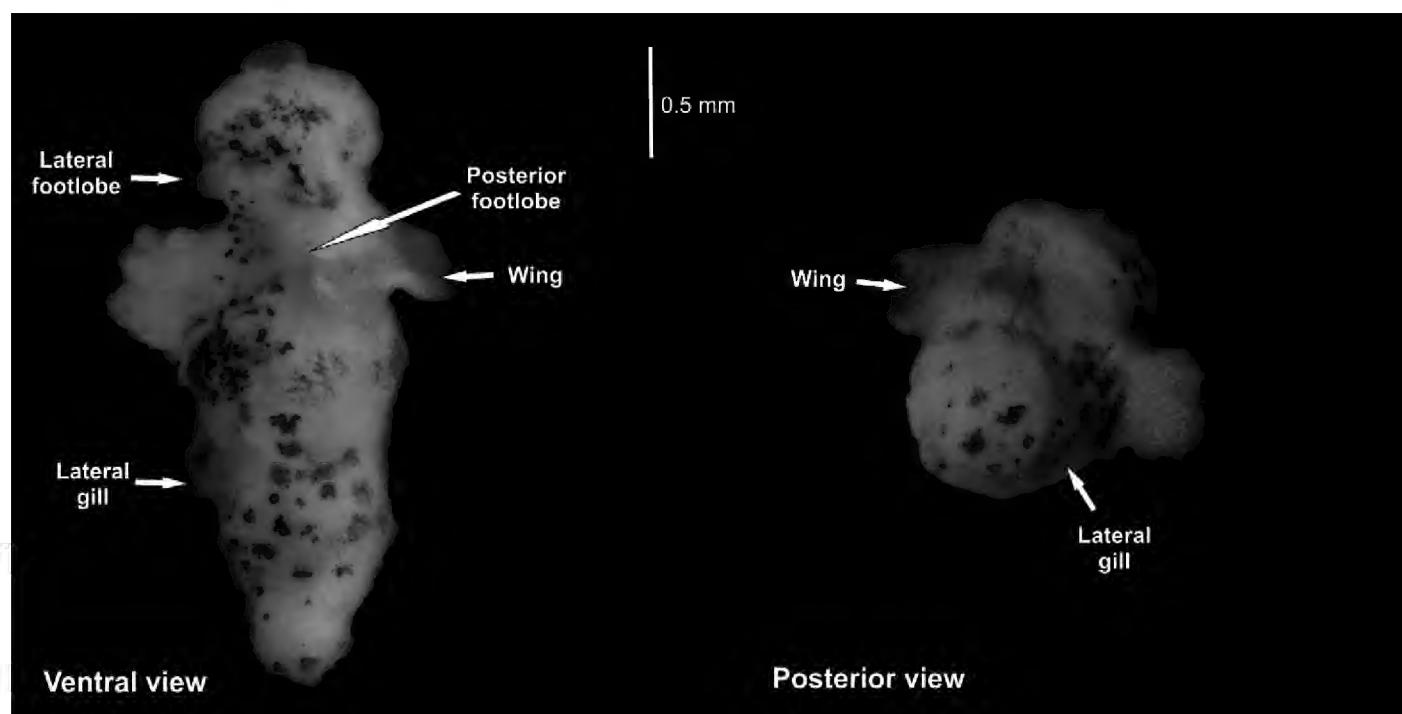


Figure 4. *Schizobrachium cf. polycotylum* Meisenheimer, 1903 (2 views). White arrows indicate diagnostic characteristics that allowed for the identification of this species.

***Spongiobranchaea intermedia* Pruvot-Fol, 1926**

Figure 3

Material examined. MEXICO – SOUTHERN GULF OF MEXICO • Campeche Canyon; 20.00°N, 092.25°W and 19.66°N, 093.50°W; 10 m and 50 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg.; CC2011-2n.

Identification. Large naked pelagic snail (3.5 mm), with a semitransparent cylindrical body and presence of chromatophores. Juvenile specimen. Two strong lateral arms, no median arm. The head parts are relatively large. The lateral footlobe is typical in size. A posterior gill and reduced lateral gill are present. Short median footlobe. Rounded lateral footlobes. Small wings. A ciliated belt is present in the middle region.

Distribution. Oceanic, epipelagic and mesopelagic in tropical, subtropical and temperate environments. Cosmopolitan (van der Spoel and Dadon 1999).

***Schizobrachium cf. polycotylum* Meisenheimer, 1903**

Figure 4

Material examined. MEXICO – SOUTHERN GULF OF MEXICO • Campeche Canyon; 20.00°N, 092.25°W and 20.75°N, 092.40°W; 10 m, 50 m, and 100 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg.; CC2011-3n.

Identification. Large organism (3.8 mm long), naked pelagic snail, with a semitransparent and cylindrical body. Two branching lateral arms with extremely small suckers; no median arm. Footlobes and wings of average in size. A posterior gill composed of two simple crests at the ventral side of the body pole. The lateral gill is reduced but present. The greatest number of suckers is found on the finest branches of the arms.

Distribution. Oceanic, epipelagic, and bathypelagic in tropical, subtropical, temperate, and sub-Antarctic environments. North Atlantic and tropical Pacific Ocean.

***Cliopsis krohnii* Troschel, 1854**

Figure 5

Material examined. MEXICO – SOUTHERN GULF OF MEXICO • Campeche Canyon; 20.00°N, 092.25°W, 20.75°N, 092.40°W and 19.66°N, 93.50°W; 10 m, 50 m, 100 m, and 200 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg.; CC2011-4n.

Identification. Organism 1.2 mm long, naked, with a globular and semitransparent body; yellowish-brown visceral mass visible. Head relatively small. Proboscis longer than the whole body. Long lateral footlobes and no median lobe, median tubercle present. Posterior gill hexagonal with four crests. Without lateral gill.

Distribution. Oceanic, epipelagic and bathypelagic in tropical, subtropical and temperate environments. Mediterranean Sea, South Atlantic: Benguela Current, North Pacific, Mexican Pacific and Indian Ocean (Seibel et al. 2007; Moreno-Alcántara et al. 2014).

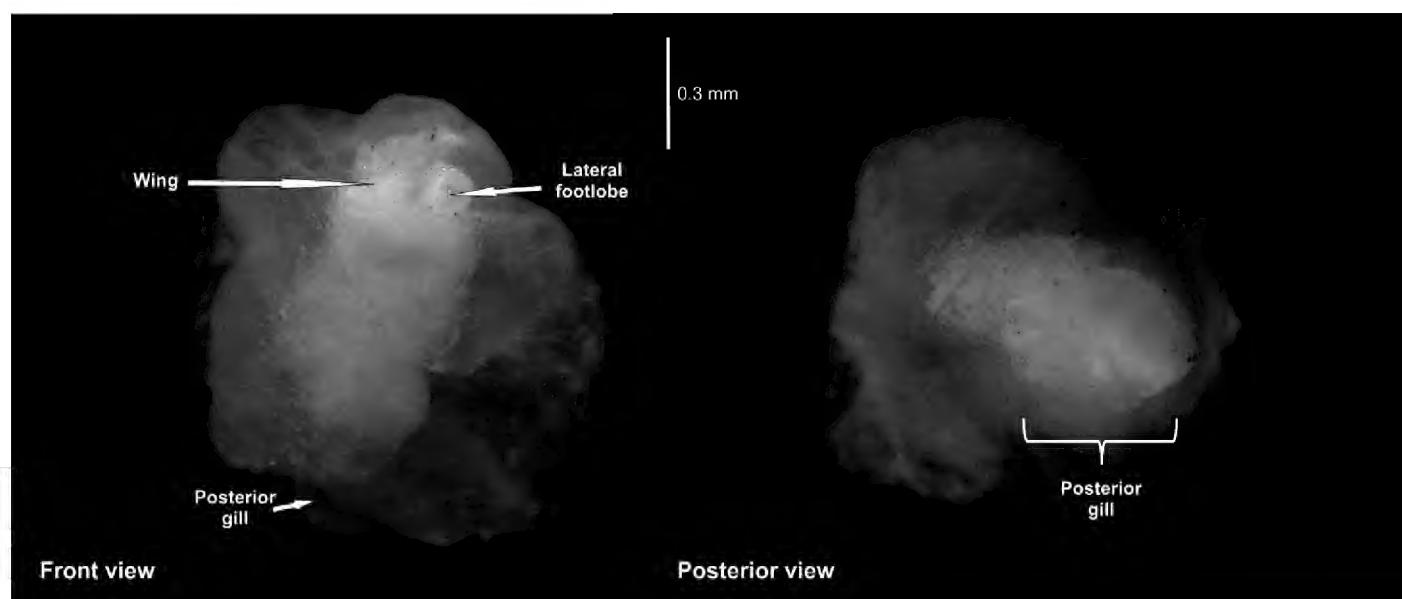


Figure 5. *Ciopsis krohnii* Troschel, 1854 (2 views). White arrows indicate diagnostic characteristics that allowed for the identification of this species.

DISCUSSION

Studies on the diversity of pteropods in the southern Gulf of Mexico began in 1970s. Since then, the importance of this group of organisms was noted because they are usually a dominant component in the region, only after copepods and chaetognaths (Toral-Almazán et al. 2022). To date, taxonomic lists include as many as 48 species from this part of the Gulf (e.g. Leal-Rodríguez 1965; Suárez 1994; Flores-Coto et al. 2013; Lemus-Santana 2014; López-Arellanes et al. 2018; López-Cabello et al. 2022).

Our study provided descriptions and illustrations of four new records of pteropods belonging to the suborder Gymnosomata and showed the hydrographic conditions at which these species were collected, which increase the knowledge of this group of organisms in the Campeche Canyon, southern Gulf of Mexico: *Pneumodermopsis macrochira*, *Spongiobranchaea intermedia*, *Schizobrachium cf. polycotylum*, and *Ciopsis krohnii*.

Pneumodermopsis macrochira has been recorded in the Gulf of California and the Mexican Pacific (Angulo-Campillo et al. 2011; Angulo-Campillo and Aceves-Medina 2018), in the Argentinian Sea (South Atlantic) (Larrazábal and Solares de Oliveira 2003), in the Sargasso Sea (Bucklin et al. 2010), and in Canada (Jennings et al. 2010). *S. intermedia* and *S. polycotylum* are well distributed in regions of the South Atlantic (van der Spoel and Dadon, 1999), while *C. krohnii* has been recorded in the southern Mexican Pacific (Moreno-Alcántara et al. 2014) and off Newfoundland (Seibel et al. 2007).

Our study also showed that the vertical distribution of the four species is quite different in relationship to the hydrographic conditions of the water column and the sampling hour (Table 1). Indeed, *Pneumodermopsis macrochira* was collected at 200 m depth, a stratum that had a temperature of 14.31 °C, whereas *Schizobrachium cf. polycotylum* was collected from 10 to 100 m depth, at temperatures ranging from 18.58 to 23.83 °C, and *S. intermedia* was collected at 10 m and 50 m depth, with temperatures of 24.5 °C and 22.9 °C, respectively. In all cases, the salinity values were relatively homogeneous (~36 g/kg) while chlorophyll-a values ranged from 0.04 to 0.93 mg/m³. This suggests a differential distribution of the four species probably related with temperature and food availability. Recent studies (e.g. Durán-Campos et al. 2017; Torres-Martínez et al. 2020) showed that the maximum chlorophyll-a in the Campeche Canyon region are deeply located (>70 m in depth), which may favor pteropods to aggregate at these specific depths. The four species reported in this study are carnivorous; however, if there is an adequate concentration of chlorophyll-a (an indicator of phytoplankton biomass), it is assumed that a bottom-up mechanism can be triggered and thus there may be food for the pteropods. This group also presents significant vertical migrations of more than 200 m in some species (Shedler et al. 2022), which explains the wide bathymetric range where these species were found.

The results presented here contribute to previous investigations, filling gaps for the coldest time of the year when the “Nortes” (winter storms) are very frequent making operations at sea quite difficult. Studies on gymnosome pteropods become especially relevant nowadays with the increased threats to the Gulf of Mexico’s ecosystems. For example, acidification, as reported by Lunden et al. (2014) represents a serious threat to this group, as mentioned above. Therefore, baseline studies become imperative to implement better management and conservation strategies of the marine resources, especially for those regions that support high biodiversity, such as the Gulf of Mexico.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions

Conceptualization: ZLC, ECM, MAMG, EDC. Data curation: ZLC, ECM, EDC. Formal analysis: ZLC, ECM, MAMG, DASDL, EDC, AG. Funding acquisition: ECM, MAMG, DASDL, EDC, AG. Investigation: ZLC, ECM, MAMG, DASDL, EDC, AG. Methodology: ZLC, ECM, DASDL, EDC. Supervision: ECM, MAMG, DASDL, EDC, AG. Project administration: ECM, MAMG, DASDL. Validation: ECM, MAMG, DASDL, EDC, AG. Writing – original draft: ZLC, ECM, MAMG, DASDL, EDC, AG. Writing – review and editing: ZLC, ECM, MAMG, DASDL, EDC, AG.

Data availability

The datasets generated during this study are available upon request to corresponding author.

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